



Rearing of Fishes in a Vegetated Littoral Zone

By K. Jack Killgore, William Pearson, and Larry G. Sanders

PURPOSE: This note provides information on the reproductive ecology of littoral fishes in a large, southeastern reservoir dominated by hydrilla (*Hydrilla verticillata*). Larval and juvenile fish assemblages were monitored for 3 years to document spatio-temporal patterns of abundance within hydrilla beds, and habitat preferences of young-of-the-year fish among different groups of aquatic plants were evaluated. Abundance of larval sunfishes was related to year-class strength among years of differing hydrilla coverage.

BACKGROUND: Larval and juvenile fish are usually more abundant in vegetated than in nonvegetated littoral zones (Barnett and Schneider 1974; Chubb and Liston 1986; Paller 1987), presumably because aquatic plants provide refugia from predators and greater food resources (Hall and Werner 1977; Gotceitas and Colgan 1987; Schramm and Jirka 1989; Savino and Stein 1989; Chick and McIvor 1994). Density and complexity of vegetation regulates distribution and abundance of young fishes (Hall and Werner 1977; Werner et al. 1977; Gotceitas and Colgan 1987; Conrow, Zale, and Gregory 1990), and some studies indicate that fish prefer certain plant species or growth forms (Werner et al. 1977; Werner, Hall, and Werner 1978; Poe et al. 1986; Conrow, Zale, and Gregory 1990; Weaver, Magnuson, and Clayton 1997).

Larval fish abundance is correlated to year-class strength (Van Den Avyle and Petering 1988, Uphoff 1989, Sammons and Bettoli 1998). Thus, vegetation has the potential to improve or maintain population integrity of littoral fishes. Consequently, aquatic plant control remains controversial even for exotic species such as hydrilla. Although high catches of young fishes in hydrilla beds have been documented (Conrow, Zale, and Gregory 1990; Chick and McIvor 1994), excessive coverage of hydrilla in the littoral zone can reduce growth and condition of juvenile and adult fishes, particularly in shallow eutrophic lakes (Colle and Shireman 1980; Wiley et al. 1984; Maceina and Shireman 1985).

Expansive, monotypic stands of hydrilla may reduce habitat quality, but any species of aquatic plant should provide nursery habitat for a variety of fish species. Contradictory studies are inevitable, however, because of seasonal changes in spatial complexity of plant beds and interspecific and ontogenetic differences in habitat preferences of the fish assemblage. These factors were addressed by measuring spatial and temporal patterns of fish reproduction in a vegetated littoral zone over a 3-year period, and by tracking year-class strength over 8 consecutive years to evaluate potential adult recruitment as a function of vegetation coverage.

METHODS: Larval fishes were collected from 1989 to 1991 in upper Lake Marion, South Carolina. Plant coverage in the 10,000-ha upper lake was greater than 4,500 ha through 1992, followed by a rapid decline to less than 100 ha by 1994 because of multiple grass carp stockings. Temporal and spatial patterns of fish abundance in hydrilla were monitored at Pack's Flats, where hydrilla was the dominant macrophyte. Fish abundance among different plant species was evaluated in Jack's Creek during 1991. Six different plant assemblages in Jack's Creek were sampled: common reed (*Phragmites australis*), pickerelweed (*Pontederia lanceolata*), water primrose

(*Ludwigia uruguayensis*), floating plants consisting of water lilies (*Nymphaea odorata*) and water shield (*Brasenia schreberi*), submersed plants consisting primarily of hydrilla with some Brazilian elodea (*Egeria densa*), and cypress trees (*Taxodium distichum*).

Larval and juvenile fishes were collected seasonally with Plexiglas light traps baited with chemical light sticks (Killgore 1994). Sampling periods corresponded to three phases of hydrilla growth patterns: late spring (April or May) when plants were rapidly growing, early summer (June) when plants began to form canopies on the water surface, and late summer (late July or August) when plants had reached their maximum density. Traps were set 30 min to 1 hr after sunset and fished for approximately 2 hr.

Spatial and temporal patterns of fishes in hydrilla were evaluated for 3 years at Pack's Flats. For each sampling period, light traps were placed along three permanent transects and fished for two consecutive nights. Transects incorporated a habitat gradient from the shoreline to the edge of plant beds. In 1991, traps were placed at Jack's Creek in the six different plant types to evaluate plant preferences of larval and juvenile fishes. Mean seasonal catch (i.e., mean number collected per 2 light trap hours) of larval and juvenile fish was calculated by year. Mean catch ($\log_{10} + 1$ transformed) was used in a repeated-measures split-plot analysis of variance (ANOVA) (Maceina, Bettoli, and DeVries 1994) to test main effects (depth, distance from shore, plant preference) while accounting for seasonal and annual interactions. If ANOVA indicated significant differences ($P < 0.05$), the Student-Newman-Keuls multiple range test (Statistical Analysis System (SAS) 1993) was used to compare main effect levels.

RESULTS AND DISCUSSION: A total of 9,296 larval and juvenile fish, representing at least 25 species, were collected in 410 light traps during the study (Table 1). Seventy-nine percent of total individuals collected were larvae. The numerically dominant taxa, representing 86 percent of total catch, were larval *Lepomis* spp., juvenile eastern mosquitofish *Gambusia holbrooki*, and larval *Enneacanthus* spp. The taxonomically dominant family was Centrarchidae. The assemblage was characteristic of vegetated littoral zones in the southeast. Most species are phytophilic as juveniles, and are facultative plant spawners (e.g., golden shiner *Notemigonus chrysoleucas*, golden topminnow *Fundulus chrysotus*, silversides, swamp darter *Etheostoma fusiforme*), or sunfishes that construct nests but prefer vegetation during one or more life stages. Compared to the 64 fish species collected in upper Lake Marion from 1988-1994 (Killgore, Kirk, and Foltz 1998), numerical dominance of larval and juvenile species was similar to that of the adult complement, except larval clupeids were under-represented in light traps.

Spatial Patterns

Habitat partitioning of fishes within littoral zones has focused on differences in depth or distance from shore (Hall and Werner 1977; Werner et al. 1977). Larval and juvenile fish are often spatially segregated in aquatic vegetation, possibly to reduce interspecific competition (Gregory and Powles 1985; Dewey and Jennings 1992) and predation risk (Crowder and Cooper 1982; Gotceitas and Colgan 1987, 1990), or as a behavioral response to food availability (Keast 1984; Werner and Hall 1988; Dionne and Folt 1991). In this study, there were no significant differences in mean catch between depths (surface and bottom) among the three seasons for the following common taxa ($\geq 0.5\%$ of total catch, Table 1): larval *Notropis* spp., larval Atherinidae, larval *Enneacanthus* spp., larval *Lepomis* spp., juvenile bluespotted sunfish, and juvenile coastal shiner.

Table 1
Number of Larval and Juvenile Fishes Collected in Upper Lake Marion, South Carolina, With Light Traps

Taxa/Life Stage	Pack's Flats			Jack's Creek 1991 93	Total Catch	Percent of Total Catch	Size Range (mm)
	1989 109	1990 133	1991 75				
Sample Size =							
Clupeidae							
Juvenile <i>Alosa</i> spp.	0	2	0	0	2	<0.1	19-33
Larval <i>Alosa</i> spp.	0	2	0	1	1	<0.1	5.4
Juvenile <i>Dorosoma cepedianum</i>	0	1	0	0	1	<0.1	16.5
Juvenile <i>D. petenense</i>	3	6	0	0	9	0.1	20-46
Larval <i>Dorosoma</i> spp.	4	7	0	0	111	0.1	4-12
Cyprinidae							
Larval common carp <i>Cyprinus carpio</i>	2	10	0	0	12	0.1	6-7
Juvenile eastern silvery minnow <i>Hybognathus regius</i>	0	1	0	0	1	<0.1	43
Juvenile golden shiner <i>Notemigonus crysoleucas</i>	1	15	2	8	26	0.3	16-38
Larval golden shiner <i>N. crysoleucas</i>	7	3	18	2	30	0.3	6-15
Juvenile coastal shiner <i>Notropis petersoni</i>	3	47	7	2	59	0.6	14-50
Larval <i>Notropis</i> spp.	94	38	30	13	175	1.9	5-15
Larval Cyprinidae	1	3	0	0	4	<0.1	6-15
Catostomidae							
Larval lake chubsucker <i>Erimyzon sucetta</i> .	1	1	10	0	12	0.1	7-15
Ictaluridae							
Juvenile channel catfish <i>Ictalurus punctatus</i>	0	2	0	0	2	<0.1	17
Aphredoderidae							
Juvenile pirate perch <i>Aphredoderus sayanus</i>	0	0	3	0	3	<0.1	30-38
Belonidae							
Juvenile Atlantic needlefish <i>Strongylura marina</i>	1	9	0	0	10	0.1	13-118
Cyprinodontidae							
Juvenile golden topminnow <i>Fundulus chrysotus</i>	0	7	11	21	39	0.4	10-53
Juvenile lined topminnow <i>F. lineolatus</i>	0	0	0	1	1	<0.1	19
Larval <i>Fundulus</i> spp.	0	8	9	24	41	0.4	5-9
Poeciliidae							
Juvenile Eastern mosquitofish <i>Gambusia holbrooki</i>	157	241	594	350	1342	14.4	9-29
Juvenile least killifish <i>Heterandria formosa</i>	6	4	30	2	42	0.5	10-23
Larval <i>H. formosa</i>	0	4	5	2	11	0.1	7-9
Atherinidae							
Juvenile brook silverside <i>Labidesthes sicculus</i>	3	11	7	6	27	0.3	10-59
Juvenile inland silverside <i>Menidia beryllina</i>	161	77	0	0	238	2.6	10-46
Larval Atherinidae	6	92	1	14	113	1.2	3-10
Percichthyidae							
Juvenile white bass <i>Morone chrysops</i>	0	1	0	0	1	<0.1	26
Centrarchidae							
Juvenile blackbanded sunfish <i>Enneacanthus chaetodon</i>	1	3	6	1	11	0.1	9-20
Larval <i>E. chaetodon</i>	0	4	1	7	12	0.1	4-6
Juvenile bluespotted sunfish <i>E. gloriosus</i>	0	9	64	41	114	1.2	9-26
Larval <i>E. gloriosus</i>	0	42	36	106	184	2.0	4-8
Larval <i>Enneacanthus</i> spp.	0	572	0	2	574	6.2	5-8
Juvenile warmouth <i>Lepomis gulosus</i>	0	1	1	12	14	0.2	11-76
Juvenile bluegill <i>L. macrochirus</i>	6	15	0	5	26	0.3	16-36
Larval bluegill <i>L. macrochirus</i>	3	8	0	0	11	0.1	5-15
Larval <i>Lepomis</i> spp.	313	5233	104	413	6063	65.2	5-14
(Continued)							

(Continued)

Table 1 (Concluded)

Taxa/Life Stage Sample Size =	Pack's Flats			Jack's Creek	Total Catch	Percent of Total Catch	Size Range (mm)
	1989 109	1990 133	1991 75	1991 93			
Centrarchidae (Continued)							
Juvenile largemouth bass <i>Micropterus salmoides</i>	0	0	6	9	15	0.2	17-35
Larval <i>M. salmoides</i>	1	4	0	0	5	0.1	6-11
Larval black crappie <i>Pomoxis nigromaculatus</i>	2	0	1	0	3	<0.1	5-6
Percidae							
Juvenile swamp darter <i>Etheostoma fusiforme</i>	0	0	0	8	8	0.1	11-24
Larval <i>Etheostoma</i> spp.	38	2	1	2	43	0.5	3-6
Totals	814	6483	947	1052	9296		

Catch of the remaining common taxa, comprised of surface-dwelling species (juvenile inland silverside *Menidia beryllina*, juvenile least killifish *Heterandria formosa*, and juvenile eastern mosquitofish), was significantly higher in surface traps during late summer. Most surface-dwelling species have alternative modes of respiration, such as gulping air, and surface access would be higher in shallow water devoid of dense, canopy-forming plants.

Catch of most juvenile and larval taxa was highest along the shoreline and declined lakeward. However, there were no significant differences in seasonal mean catch of juvenile coastal shiner and juvenile bluespotted sunfish at different distances from shore, indicating ubiquitous distribution within plant beds. Juvenile inland silversides were the only taxa whose catch was significantly higher in the middle and edge of the plant beds during the summer. Silversides are known to exhibit diel inshore-offshore movements (McComas and Drenner 1982), which may account for their lakeward location.

Many small species, such as topminnows and live-bearers, characteristically occur near the shoreline to avoid predation or because they prefer shoreline substrates (Werner, Hall, and Werner 1978; Meffe and Snellson 1989). Paller (1987) found that larval and juvenile fishes were 160 times higher in macrophytes than in open channels, and most larvae concentrated in the interior of the bed rather than at the edge, possibly feeding on midges and zooplankton that were more abundant in plants. Similarly, Guillory, Jones, and Rebel (1979) reported that mosquitofish and least killifish preferred shallow, densely vegetated areas, whereas *Enneacanthus* spp. were more common in dense beds further from shore.

Temporal Patterns

Species richness and total catch in Pack's Flats were highest during 1990 (Table 1). Of the ten most common taxa in Pack's Flats, mean catch of larvae was significantly higher in 1990 with two exceptions: larval *Notropis* spp. was not significantly different among years and larval *Etheostoma* spp. was significantly higher in 1989. Conversely, mean catch of juveniles was significantly higher in 1991 with two exceptions: juvenile inland silversides were absent in 1991 and juvenile coastal shiners were not significantly different among years.

Percent abundance of juveniles was higher in late summer, whereas abundance of larvae varied among species and seasons (Figure 1). Early spawning groups included cyprinids, silversides, and darters. However, larval *Notropis* spp. and Atherinidae were probably comprised of several species

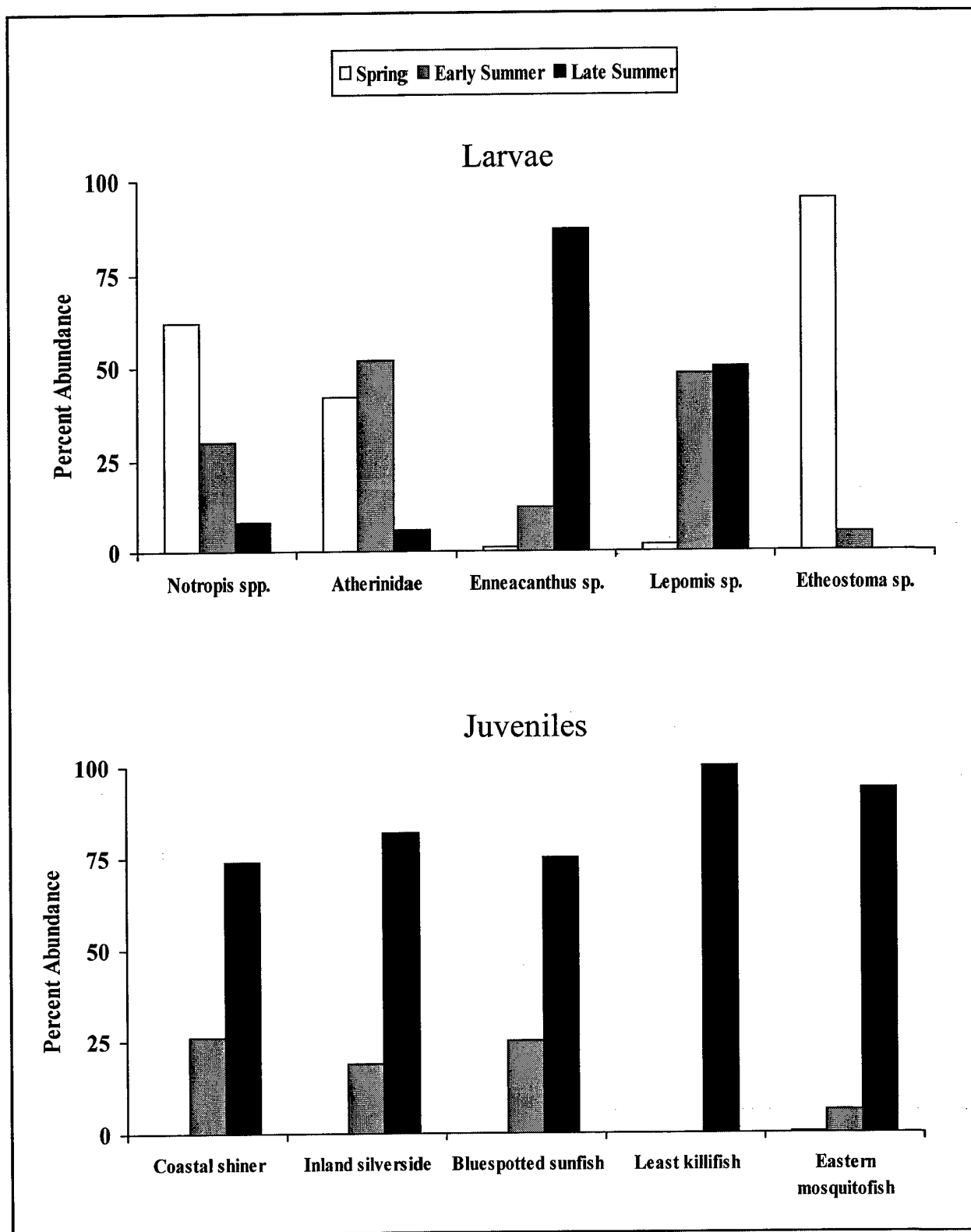


Figure 1. Seasonal abundance of larval and juvenile fishes collected in Pack's Flats, upper Lake Marion, South Carolina, from 1989 to 1991

that contributed to prolonged appearance of larvae during summer. Larval *Etheostoma* spp. were almost exclusively collected in spring. Summer spawners included larval *Lepomis* spp., probably

comprised of several species, and this group was almost equally abundant in early and late summer. Larval *Enneacanthus* spp. were most abundant in late summer.

High catches of larval fishes in 1990, particularly nest-building sunfishes, may have been related to the devastating effects of Hurricane Hugo the previous autumn. The hurricane passed over Lake Marion in October 1989 and ensuing floods scoured large areas of the lake, uprooting hydrilla, and apparently suppressing plant growth during the peak nesting period of sunfishes. However, plant coverage was similar to pre-hurricane levels by June 1990. Fish denude nest areas of vegetation, even to the point that patterns and zonation of submersed macrophytes are influenced (Carpenter and McCreary 1985), but dense vegetation can decrease the availability of nesting sites (Smith and Crumpton 1977; Colle and Shireman 1980). Therefore, expansion of nonvegetated nesting sites in spring 1990 likely led to higher spawning success of sunfishes.

Plant Preferences

Aquatic plant species have different effects on water chemistry (Frodge et al. 1990), exhibit distinctive growth forms or architecture (Dionne and Folt 1991, Lillie and Budd 1992; Dibble, Dick, and Killgore 1996; Chick and McIvor 1994), and may harbor different invertebrate assemblages (Chilton 1990; Lalonde and Downing 1992; Beckett, Aartila, and Miller 1992), all of which can affect habitat selection of fishes. Furthermore, ontogenetic changes in habitat use patterns of fishes are extensively documented (e.g., Hall and Werner (1977); Werner and Hall (1988); Scott and Nielson (1989)) indicating that the relationship between habitat preference and vegetation may differ among life stages.

In our study, larval fish were more common (>70 percent) in reeds, submersed plants, and cypress trees, whereas juvenile fish were more common in pickerelweed, water primrose, and floating plants. Other studies have shown high utilization of submersed plants by larval fish whereas juvenile fish, particularly topminnows and mosquitofish, prefer emergent types of vegetation (Poe et al. 1986, Dewey and Jennings 1992, Chick and McIvor 1994). Of the most common taxa, mean annual catch of juvenile eastern mosquitofish was significantly higher in water primrose, although this species was widely distributed among all plant types (Table 2). There were no overall significant differences in mean annual catch for larval *Enneacanthus* spp. or juvenile bluespotted sunfish, although both were more abundant in reeds during spring and early summer, and juvenile bluespotted sunfish abundance was highest in cypress trees during late summer (Figure 2).

Table 2
Mean (\pm SD) Annual Catch of Larval and Juvenile Fishes in Six Different Plant Types in Jack's Creek, Lake Marion, 1991 (asterisk indicates that catch of a taxa in a plant type was significantly higher ($P \leq 0.05$) according to Student-Neuman-Keuls test)

Plant Type	N	Eastern Mosquitofish Juveniles	<i>Lepomis</i> spp. Larvae	Bluespotted Sunfish Juveniles	<i>Enneacanthus</i> spp. Larvae
Reeds	9	1.33 \pm 1.22	0.11 \pm 0.33	0.44 \pm 1.33	5.11 \pm 15.33
Pickerelweed	11	1.00 \pm 1.18	0.36 \pm 0.67	0.36 \pm 0.67	0.27 \pm 0.65
Water primrose	20	6.45 \pm 8.58*	0.45 \pm 1.00	0.15 \pm 0.37	0.75 \pm 1.33
Floating plants	20	2.80 \pm 3.22	0.25 \pm 0.55	0.55 \pm 0.94	0.55 \pm 1.10
Submersed plants	20	4.40 \pm 4.72	7.35 \pm 12.17*	0.30 \pm 0.73	1.50 \pm 1.99
Cypress trees	13	4.15 \pm 4.86	19.00 \pm 41.07*	1.00 \pm 2.00	0.23 \pm 0.60

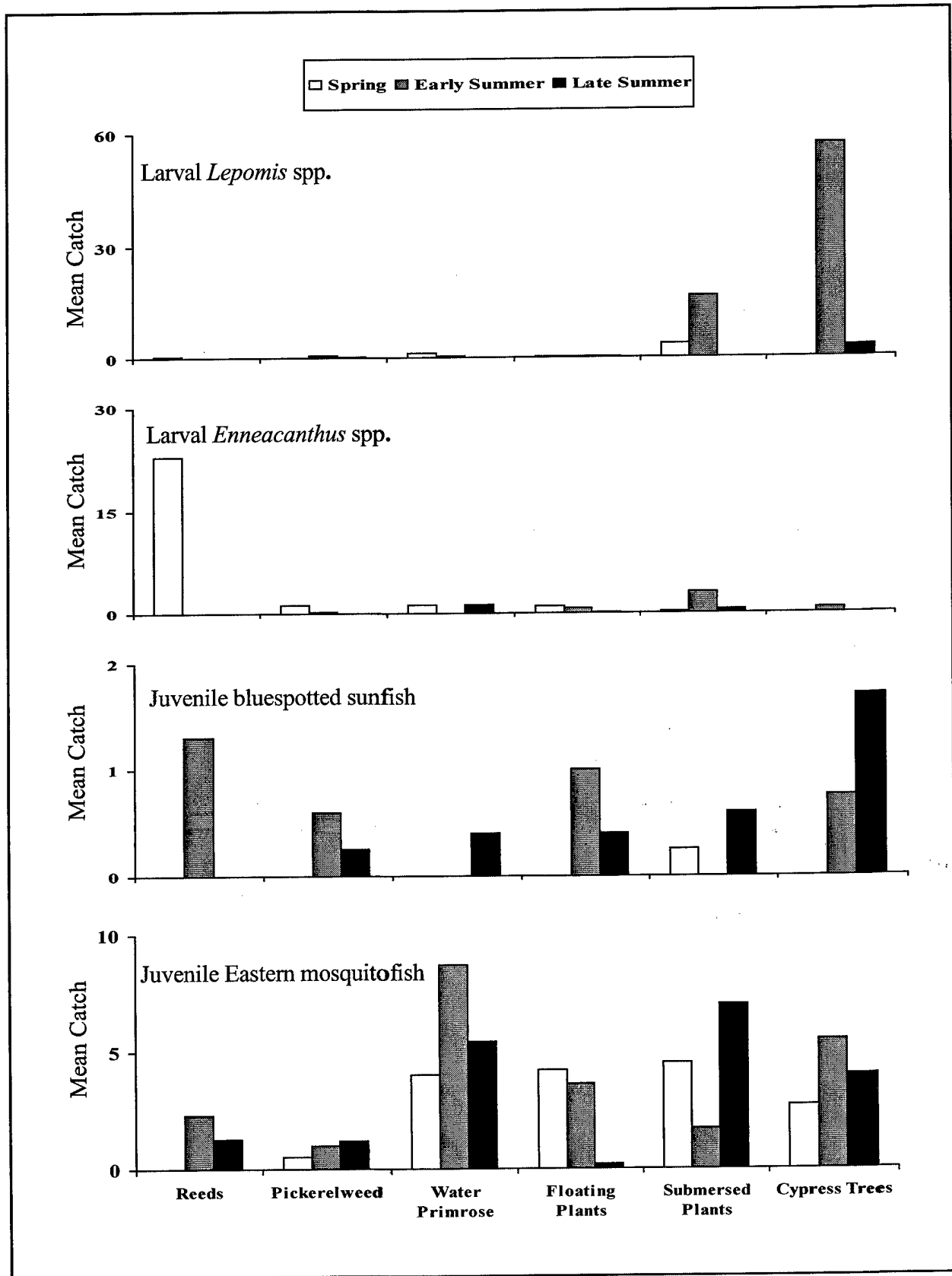


Figure 2. Seasonal mean catch (number per 2 hours of light trapping) of common fishes collected during 1991 in six different plant types in Jack's Creek, upper Lake Marion, South Carolina

Juvenile fishes are often ubiquitous in vegetated littoral zones (Guillory, Jones, and Rebel 1979; Conrow, Zale, and Gregory 1990), but larvae may be more selective because of limited motility and higher susceptibility to predation. This may apply to larval *Lepomis* spp., which in this study was significantly more abundant in submersed plants and cypress trees (Table 2). On a seasonal basis, mean catch of larval *Lepomis* spp. was highest in cypress trees during early summer even though submersed plants were considerably more widespread (Figure 2). Stands of cypress trees can form structurally complex habitats by their aggregation of cypress knees, branches, and vegetation. Since structural diversity is more important to fishes than the amount of vegetation (Eadie and Keast 1984; Conrow, Zale, and Gregory 1990; Dewey and Jennings 1992), cypress trees can provide greater habitat value to rearing fishes than monospecific stands of submersed vegetation.

CONCLUSIONS AND MANAGEMENT IMPLICATIONS: Most larvae and surface-dwelling juvenile species preferred shoreline habitats or the interior of submersed plant beds, and their seasonal abundance in these habitats corresponded to their spawning chronology. In general, juveniles were more ubiquitous than larvae, but this particular study evaluated nocturnal patterns, which may differ during the day because of inshore-offshore diel movements of young fishes (Emery 1973, Paller 1987).

Multiple species of emergent vegetation and shallow water near the shoreline create a diverse habitat preferred by young and small fishes. Shoreline habitats may become more important when dense stands of submersed plants become established because they are less vegetated and the shallow water serves as a refugium from larger predators. Although larval and juvenile fishes utilize hydrilla as rearing habitat, data from this study suggest that the habitat value of dense plant beds declines over the growing season. Early emergence of hydrilla provides structure in a relatively unstructured landscape during the spring, but once dense canopies form, larval fish became more abundant in cypress trees possibly to avoid competition, low dissolved oxygen, and predation. The presence of fish in hydrilla may be partly due to its widespread distribution rather than active selection by the fish, but cypress trees are considerably less abundant than hydrilla, suggesting that fish prefer large, woody habitats during rearing.

A study of juvenile and adult fishes in Lake Marion following introduction of grass carp concluded that there were no major changes in littoral fish abundance once hydrilla began to decline (Killgore, Kirk, and Foltz 1998). The presence of other structures, such as cypress trees, was invoked as a contributing factor. This study also suggests that cypress trees, as well as emergent vegetation, provide similar habitat value to early life history stages of fishes as submersed plants.

Year-class strength of fishes is usually established before the end of a cohort's first growing season (Diana 1995). In Lake Marion, the continued availability of cypress trees and emergent vegetation as rearing habitat following decline of hydrilla probably contributed to strong year-classes of littoral fish populations. In addition, suppression of plant growth in the littoral zone during spring 1990, due to floods created by Hurricane Hugo the previous year, and eventual decline of hydrilla system-wide, expanded the availability of unvegetated nesting sites. This is illustrated by tracking relative abundance of age-1+ sunfishes from 1989 – 1995 (Killgore, Kirk, and Foltz 1998). In 1992, abundance of age-1+ bluegill, redear sunfish, and blackspotted sunfish increased following the peak catches of larval sunfishes in 1991 (Figure 3). Furthermore, once hydrilla began to decline in 1992, there was a disproportionate increase in age-1+ sunfishes the following 2 years. Although hydrilla

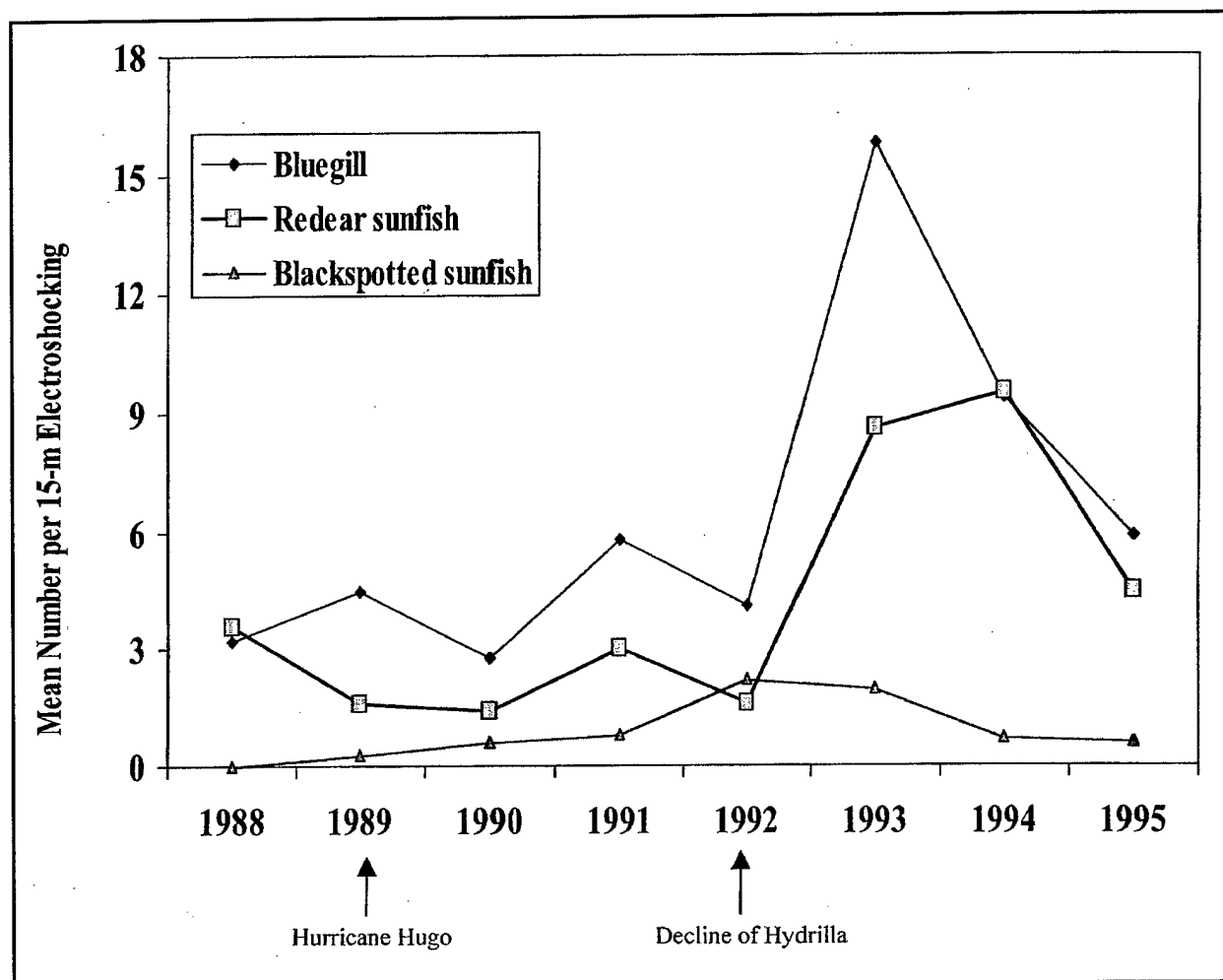


Figure 3. Mean number of age-1+ sunfishes collected by electroshocking in upper Lake Marion from 1988 to 1995 (Killgore, Kirk, and Foltz 1998) in relation to Hurricane Hugo and system-wide decline of hydrilla

is difficult to control throughout the growing season, results indicate that suppressing plant growth during the spring may lead to higher reproductive success and recruitment of nest-building species.

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